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Evaluation of selection indices in a recurrent selection program in corn (Zea mays L.)

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Iowa State University, 1989

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Evaluation of selection indices in a recurrent selection program in corn (*Zea mays* L.)

by

Julio Hernando Milla

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INTRODUCTION

Corn breeders are generally interested in improving more than one trait at a time, or improving one trait without affecting the performance of others. When single-trait selection is practiced and the correlation of that trait with others is high and unfavorable, undesirable correlated responses may occur for those traits not being considered in the selection criteria. Martin and Russell (1984) reported that three cycles of selection for mechanical stalk breakage and resistance to Diplodia stalk rot in corn resulted in populations with significantly reduced yields. They suggested that simultaneous selection for stalk quality and yield would be the most practical scheme to follow to avoid deleterious responses in yield. Klenke et al. (1986) also reported that four cycles of selection for European corn borer [Ostrinia nubilalis (Hubner)] resistance resulted in a yield reduction. Based on this result, they suggested that yield should be included in the selection criteria during selection for European corn borer resistance. Willman et al. (1987) evaluated genotypic variation and effect of environment on 21 plant traits and determined the relationship of those traits to grain yield and stalk lodging in corn. They concluded that the relationship between plant traits and productivity is complex and suggested that the use of a single-plant trait in

a breeding program would likely be ineffective in improving grain yield and/or stalk lodging resistance of corn.

Three methods have been used to simultaneously improve several traits: tandem selection, independent culling and index selection. The latter, as indicated by Hazel and Lush (1942), is the most efficient method for improving several quantitative traits simultaneously. Several types of selection indices have been developed. The first one formally introduced, and probably the most widely known, is the so called Smith-Hazel index (Smith, 1936; Hazel, 1943). Among others that followed are the base and weight-free indices.

One of the requirements for using the Smith-Hazel index is the estimation of phenotypic and genotypic variances and covariances (Lin, 1978; Baker, 1986). Sampling errors on the estimation of these parameters could affect the reliability of the index (Lin, 1978) and, consequently, limit the use of this type of selection index. Several researchers (Brim et al., 1959; Hallauer and Miranda, 1988; Kauffman and Dudley, 1979; Suwantaradon et al., 1975) have suggested that these parameter estimates could be improved by pooling information over different cycles of selection, compared to using the data pertaining to the specific cycle of selection. Drawbacks from this approach have been also anticipated. Manning (1956) has argued that using data from the particular cycle of selection may be more effective because the weighting of several traits

in an index is a function of the exact environmental conditions in which the crop was raised. Also, Hallauer and Miranda (1988) stated that if significant changes in gene frequency are suspected then estimates from the most recent cycle of selection should be used.

The objectives of this study are: 1) to compare the effectiveness of different selection index methods on the simultaneous improvement of grain yield, grain moisture, root lodging and stalk lodging in corn; and 2) to evaluate the effect of pooling phenotypic and genotypic variances and covariances over several cycles of selection on the estimation of a selection index for improving grain yield, grain moisture, root lodging and stalk lodging in corn.

LITERATURE REVIEW

Selection Index Theory

The selection index is a procedure that provides a single criterion for selection among genotypes by including combinations of several traits. The objective of a selection index is to find a linear combination of phenotypic values that maximizes the expected gain in aggregate genotype (Hallauer et al., 1988). The selection index and the aggregate genotype are defined as (Lin, 1978):

$$\text{Index:} \quad I = \Sigma_{i}^{n} = {}_{1}b_{i}x_{i}$$

$$\text{Aggregate genotype:} \quad H = \Sigma_{i}^{n} = {}_{1}a_{i}g_{i}$$

where n is the number of traits in the index; x_i is the observed phenotypic value of the i-th trait; b_i is the weight assigned to the i-th trait in the selection index; g_i is the unobservable genotypic value of the i-th trait; and a_i is the relative economic value of the i-th trait.

Smith (1936) proposed a general method for handling more than one trait at a time in a plant breeding program. He developed a selection index based on a linear combination of phenotypic values weighted in such a way that expected gain in aggregate genotypic value would be maximized. The weights are calculated using information on 1) the economic value of each trait; and 2) the phenotypic and genotypic variances of each

trait and the respective covariances among traits.

The same index was also proposed by Hazel (1943), but using estimated values for phenotypic and genotypic parameters. He presented the genetic basis for the construction of selection indices and outlined methods for estimating the required variances and covariances. This index is now known as the Smith-Hazel index (Hallauer et al., 1988).

Two other methods of selection are recognized as appropriate for simultaneous improvement of more than one trait, these are independent culling and tandem selection. Independent culling requires the specification of levels of merit for each trait, an individual with a phenotypic value below this minimum level for any trait is not selected. With tandem selection, the traits are selected one at a time until they are improved to the desired level. Once a trait reaches that desired level of improvement, selection begins on the next trait and so on until all traits have been improved (Baker, 1986).

Hazel and Lush (1942) evaluated the relative efficiencies of these three methods of multiple trait selection. They showed that, for uncorrelated traits with equal economic importance, the index selection method is most efficient, while the tandem selection method is the least efficient of the three. The expected genetic gain in any one trait from selection on an index containing (n) traits is $1/(n)^{1/2}$ times

as large as selection for that trait alone.

Young (1961) also evaluated these selection methods and obtained similar results. He concluded that, when traits are independent and not of equal importance, index selection is more efficient than tandem selection. The superiority of index selection over independent culling was greatest when the traits were of equal importance and selection intensity was low or intermediate. Baker (1986) indicated that generalization of the results from these studies is difficult but it seemed that selection using the optimum index would always be at least as effective as selection based on independent culling which, in turn, should always be at least as effective as tandem selection.

In theory, index selection maximizes the genetic gain in the aggregate genotype, but it does not necessarily produce simultaneous improvement in each trait included in the index. Index selection may even lead to undesirable changes in some traits. Consequently, modifications to the selection index have been proposed.

Kempthorne and Nordskog (1959) developed the restricted selection index in which the genetic gain in some traits is maximized while restricting change in other traits to zero. Tallis (1962) proposed a method where certain traits will be improved by a fixed amount, while the gain in others is maximized. He gave a mathematical solution to this problem by

constructing a selection index to maximize gain in the aggregate genotype subject to r restrictions.

Pesek and Baker (1969), considering the problem of assigning relative economic weights to the traits, proposed the use of desired gains instead of the economic weights. This is basically the same method proposed by Tallis (1962) when the number of restrictions is the same as the number of traits being considered in the index. Tai (1977) also proposed a method of constructing selection indices based on the desired gains for traits with economic importance. He suggested that secondary traits with no economic importance may also be included in the index to assist selection. In that case, their economic weights are set to zero.

Sampling errors in the estimation of phenotypic and genotypic variances and covariances and the effect of those errors on the accuracy of the selection index has motivated the development of other indices in which these parameter estimates are not needed. Also, improvement of these parameter estimates by pooling information from different cycles of selection has been suggested (Brim et al., 1959; Suwantaradon et al., 1975; Kauffman and Dudley, 1979).

Brim et al. (1959) suggested weighting each trait by the relative economic value when sampling errors of parameter estimates are large. Williams (1962) evaluated this index and named it the base index. He stated that the foremost

attribute of this index is its simplicity of construction and interpretation. He also indicated that if the parameter estimates deviate only slightly from their true values, then the use of the estimated index is advisable when it provides a worthwhile improvement over alternative indices. The advantages of the base index over the estimated Smith-Hazel index are simplicity, freedom from errors of parameter estimation, and the index can be constructed when population parameter estimates are not available (Lin, 1978).

The multiplicative (Elston weight-free) index developed by Elston (1963) and the rank summation (Mulamba and Mock, 1978) indices are parameter free methods, with the advantage that they are weight-free. The multiplicative index is constructed by subtracting the minimum sample value for each trait and forming the product of the adjusted values. The rank summation index is calculated by ranking the genotypes for the traits of interest and then summing the ranks over traits.

Use of Selection Indices in Corn

Selection indices can be used to improve the efficiency of selection for a single quantitative trait, either by incorporating information from correlated traits or

by measuring the same trait in relatives. The most common use of selection indices is for the improvement of two or more traits simultaneously (Baker, 1986). There are several published and unpublished examples of the evaluation and use of selection indices in breeding programs for either of these two objectives.

Robinson et al. (1951) constructed a selection index to improve the efficiency of selection for grain yield in corn; they showed that indices involving different combinations of yield, yield components and plant height resulted in greater expected response than direct selection for yield. Yousaf (1976) compared selection indices for various combinations of yield and its components (ear index, number of rows of kernels, number of kernels per row and 100-kernel weight) on the basis of expected genetic gain. Selection for yield based on the index using all five characters was expected to be 12% more efficient than selection for yield alone. This efficiency was still maintained after dropping number of kernels per row from the index.

Subandi et al. (1973) compared the efficiencies of five selection indices (three weight-free and two Smith-Hazel) using yield, percentage of lodged plants and percentage of dropped ears in two variety crosses of corn. A multiplicative and one of the Smith-Hazel indices gave about the same total gain in machine-harvestable yield. The multiplicative index

was recommended over the Smith-Hazel because of its simplicity.

Widstrom (1974) constructed three selection indices to aid in selection for resistance to ear damage caused by corn earworm. The traits included were corn earworm injury, husk tightness, days to 50% pollen shed, and husk extension. The indices were: 1) a Smith-Hazel index (RS) constructed in the traditional manner, 2) a Smith-Hazel index (RI) constructed using the direct and correlated responses to selection instead of the genotypic variances and covariances, respectively, and 3) a base index (RSI) with the standardized direct and correlated responses when selection was for corn earworm injury as index weights. The response to four cycles of S_1 recurrent selection using these three selection indices was evaluated by Widstrom et al. (1982). Their results indicated that none of the indices were superior to conventional selection for resistance to corn earworm, but the RI index was judged to compare most favorably when considering all trait responses. The RI index gave better results than RS and RSI.

Several studies have been conducted to evaluate the efficiency of selection indices for the simultaneous improvement of more than one trait in corn (Suwantaradon et al., 1975; Kauffman and Dudley, 1979; St. Martin et al., 1982; Crosbie et al., 1980; Smith et al., 1981a; Motto and Perenzin, 1982). Suwantaradon et al. (1975) compared a Smith-Hazel

index, a base index and a desired gain index for the simultaneous improvement of seven traits in corn. The Smith-Hazel and the base indices gave similar results, and the authors suggested using the base index if the relative economic values were known. The desired gain index would be preferred if relative economic values were difficult to specify. Kauffman and Dudley (1979) compared the effectiveness of a desired gain index, direct selection and a Smith-Hazel index for the simultaneous improvement of corn grain yield and protein percentage. Seven selection method-index combinations were considered. The desired gain index was suggested as being effective for the simultaneous improvement of both traits. Motto and Perenzin (1982) evaluated two Smith-Hazel indices and the desired gain index. They concluded that the use of selection indices, and particularly the use of a desired gain index, appears useful for the simultaneous improvement of grain yield and protein content in corn.

Crosbie et al. (1980) compared several selection indices based on selection differentials, expected gains, and relative efficiencies of cold tolerance traits. They concluded that the best results for all traits were given by the rank summation, the multiplicative, and a base index (index weights were reciprocals of phenotypic standard deviations). These indices were not seriously affected by unequal variances among

traits. Other indices, such as the base and Smith-Hazel that were computed by using equal economic weights, placed the most emphasis on the trait with the largest genetic variance which impeded the maximization of gain for each trait in the index.

Smith et al. (1981a) evaluated three selection indices for improving grain yield, root lodging, stalk lodging and percent grain moisture; one that used heritabilities as index weights, the base index and the Smith-Hazel index. Equal economic values were used for the four traits. The product of heritabilities and economic weights as index weights ($b_i = a_i h_i^2$) for each trait are the same solutions from the optimum index if the traits are uncorrelated (Hazel, 1943). They included this type of index in their study because the correlations among the traits they were considering were low ($|r| < .3$). The index that used heritabilities as index weights was recommended because for the data examined the correlations were low and the heritabilities were computed in routine data analyses and were available at no additional cost. In addition, this index resulted in little predicted loss of efficiency (< 1%), when compared with the Smith-Hazel index, and selection for the individual traits was in the desired direction.

St. Martin et al. (1982) evaluated several restricted selection indices for the improvement of opaque-2 corn. They concluded that the use of selection indices for multiple-

trait improvement probably requires a measure of subjective judgement by the breeder. This agrees with the statement given by Smith et al. (1981b): "We doubt that the use of a selection index will take the "art" out of plant breeding; it may however, make us more aware of some of the methods being used and provide a useful tool in practicing this art".

There have been few published reports on the use of selection indices in recurrent selection programs in corn. The multiplicative index has been applied to several recurrent selection schemes conducted by the University of Nebraska corn breeding project since 1968. Their objective has been to improve grain yield, reduce the proportion of plants lodged and reduce the number of dropped ears (Compton and Lonnquist, 1982). West et al. (1980) indicated that the multiplicative index has proved its ability to simultaneously improve the traits involved. Odhiambo and Compton (1989) reported that after five cycles of selection using this index, significant increases have been found for index and yield in two out of three populations under improvement and ears per plant were increased in all three populations. They indicated that these results are a measure of the value of this type of index in selection studies.

Pani et al. (1985) evaluated the response to phenotypic selection for four seed quality traits (protein content, dye binding capacity, tryptophan content, and specific weight),

using a base index during four cycles of selection. The rate of progress for the four traits was nearly linear. Mulamba and Mock (1978) reported that selection using rank summation index for leaf orientation rating, leaf area per plant, and pollen-shed-to-silking interval would change these three traits in the desired direction. Moreover, selection for these traits would promote yield improvement.

In general, the majority of researchers that have either compared or used selection indices in corn have favored the use of indices that are parameter free and/or weight free. The use of any selection index in corn improvement will depend on the goals of the breeding program and also on the interrelationships that may exist among the traits under selection. If the objective is to select those individuals or families with the highest aggregate genotype then, in theory, the Smith-Hazel index would be the best index to use. However, if simultaneous improvement in several traits is desired other alternative indices could be more appropriate than the Smith-Hazel.

Explanation of Thesis Format

This dissertation is comprised of an introduction, literature review, Section I titled "Comparison of Different Selection Indices in a Recurrent Selection Program in Corn

(*Zea mays* L.).", Section II titled "Effect of Pooling Variances and Covariances over Several Cycles of Selection on the Estimation of a Selection Index."

Each section constitutes a manuscript to be submitted to a professional journal. Following Section II, a General Summary is included.

SECTION I. COMPARISON OF DIFFERENT SELECTION INDICES IN A RECURRENT SELECTION PROGRAM IN CORN

Abstract

Plant breeders are generally interested in simultaneously improving several traits, or improving one trait without affecting the performance of others. One way of selecting for more than one trait at a time in a breeding program is through index selection. The objective of this study was to evaluate several selection indices in corn for the simultaneous improvement of grain yield, grain moisture, root lodging, and stalk lodging.

The indices evaluated were three of the Smith-Hazel type, the corresponding base indices, the Smith 1981-type when genotypic and phenotypic correlations are considered to be zero and two weight free indices (multiplicative and rank summation). All indices were compared by using selection differentials, expressed as a percentage of the selection differentials obtained when single-trait selection was practiced, and predicted genetic gains for each of the traits. For determining similarities among indices, rank correlations and percentage of selected lines in common were calculated for all pairs of indices. The indices were calculated for five cycles of half-sib family selection and six cycles of

selfed family selection conducted in the Iowa Stiff Stalk Synthetic population.

There were variations in the genotypic and phenotypic correlations across cycles for both recurrent selection schemes. The selection differentials obtained for each trait varied across cycles and for the different selection indices. In some instances very low and even selection differentials in the unfavorable direction were obtained. The predicted genetic gains behaved similarly to the selection differentials. Similarities, based on the rank correlations and percentage of lines selected in common, were found among some selection indices. From the results of this study we concluded that the degree of improvement on each of the traits was influenced by the structure of the correlations between traits. In general, the selection indices most influenced by correlations were those requiring estimates of phenotypic and genotypic parameters. The base index using the reciprocal of the phenotypic standard deviations of the traits as index weights, and the two weight free indices were less affected by the correlation structure, resulting in a more even improvement for the four traits considered.

Introduction

Plant breeders are generally interested in improving more than one trait at a time, or improving one trait without affecting the performance of others. Hallauer and Miranda (1988) indicated that if recurrent selection is used, the simultaneous selection for several traits is necessary. In order to improve a population, several traits must be considered at the same time, populations with good performance for some traits but undesirable for others will not be considered as useful for direct use or for the extraction of improved genotypes from them. When single-trait selection is practiced and the correlation of that trait with others is high and unfavorable, undesirable correlated responses may occur for those traits not being considered in the selection criteria. In this case, multiple-trait selection becomes indispensable. Reliability and simplicity are the main prerequisites for the use of a selection index in germplasm improvement programs.

In 1936, H. F. Smith proposed a general method for handling more than one trait at a time in a plant breeding program. He developed a selection index based on a linear combination of phenotypic values weighted in such a way that the expected genotypic value was maximized. The same index was also proposed by Hazel (1943) using estimated values for

the phenotypic and genotypic parameters. This index is now known as the Smith-Hazel index (Hallauer et al., 1988).

In the calculation of this index, estimates of phenotypic and genotypic variances and covariances are needed. Sampling errors in the estimation of these parameters and the effect of those errors on the accuracy of the selection index has motivated the development of other indices, which do not require the use of these paramenters. Brim et al. (1959) suggested weighting each trait by the relative economic value when sampling errors of parameter estimates are large. Williams (1962) evaluated this index and named it the base index. He stated that the foremost attribute of the base index is simplicity of construction and interpretation.

Because economic values of the different traits included in the index are sometimes difficult to define, selection indices that are weight-free have been developed (Elston, 1963; Mulamba and Mock, 1978). Elston (1963) proposed the multiplicative index which is constructed by subtracting the minimum sample value for each trait and forming the product of the adjusted values. Mulamba and Mock (1978) developed the rank summation index which is calculated by ranking the genotypes for the traits of interest and then summing the ranks of each trait. Another advantage of these two indices, besides being weight-free, is that phenotypic and genotypic variances and covariances are not needed in their calculation.

Also, due to the difficulty of defining economic values, the relative "economic values" have been assigned based on estimating parameters such as the heritability or phenotypic standard deviation of the traits involved in the index (Young, 1961; Crosbie et al., 1980). Young (1961) showed that the superiority of index selection over tandem selection and independent culling increases with decreasing differences in relative importance among traits selected. The relative importance (T) of a trait is given by $T_i = a_i h_i^2(SD_i)$ where a_i, h_i^2 and SD_i are the economic value, the heritability and the phenotypic standard deviation of the i-th trait, respectively. If equal relative importance is assigned to each trait, T_i will be a constant and the relative economic value for the i-th trait is $a_i = T/h_i^2(SD_i)$. Crosbie et al. (1980) evaluated several indices for the improvement of cold tolerance traits in corn. One of the indices evaluated was a base index in which the "economic values" were the reciprocals of the phenotypic standard deviations for each trait. They found that this index produced good selection differentials and predicted gains in each trait and in the aggregate genotype across populations and cycles of selection used in their study.

Several studies have been conducted to evaluate the efficiency of selection indices for the simultaneous improvement of more than one trait in corn (Suwantaradon et

al., 1975; Kauffman and Dudley, 1979; St. Martin et al., 1982; Crosbie et al., 1980; Smith et al., 1981a; Motto and Perenzin, 1982). Suwantaradon et al. (1975) compared a Smith-Hazel index, a base index and a desired gain index for the simultaneous improvement of seven traits in corn. The Smith-Hazel and the base indices gave similar results and the authors suggested using the base index if the relative economic values were known. The desired gain index would be preferred if relative economic values were difficult to specify. Kauffman and Dudley (1979) compared the effectiveness of a desired gain index, direct selection and a Smith-Hazel index for the simultaneous improvement of corn grain yield and protein percentage. Seven selection method-index combinations were considered. The desired gain index was suggested as being effective for the simultaneous improvement of both traits. Motto and Perenzin (1982) evaluated two Smith-Hazel indices and the desired gain index. They concluded that the use of selection indices, and particularly the use of a desired gain index, appears useful for the simultaneous improvement of grain yield and protein content in corn.

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Smith et al. (1981a) evaluated three selection indices for improving grain yield, root lodging, stalk lodging and percentage grain moisture; the base index, the Smith-Hazel index and a modified Smith-Hazel index that used heritabilities as index weights. They were interested in the latter index because this index is the solution obtained for the optimum index (Smith-Hazel) when the correlations among traits are zero. The modified Smith-Hazel index is a good approximation to the optimum index when the correlations are small ($|r| < .3$). They assigned equal economic values to the four traits included in the selection indices. The modified Smith-Hazel index resulted in little predicted loss of efficiency (< 1%) when compared with the Smith-Hazel index, and selection for the individual traits was in the desired direction. They recommended the modified Smith-Hazel index for the simultaneous improvement of grain yield, root lodging, stalk lodging and percentage grain moisture.

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selection indices for the improvement of opaque-2 corn. They concluded that the use of selection indices for multiple-trait improvement probably requires a measure of subjective judgement by the breeder. This agrees with the statement given by Smith et al. (1981b): "We doubt that the use of a selection index will take the "art" out of plant breeding; it may however, make us more aware of some of the methods being used and provide a useful tool in practicing this art".

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selection for four seed quality traits (protein content, dye binding capacity, tryptophan content, and specific weight), using a base index during four cycles of selection. The rate of progress for the four traits was nearly linear. Mulamba and Mock (1978) reported that selection using rank summation index for leaf orientation rating, leaf area per plant, and pollen-shed-to-silking interval would change these three traits in the desired direction. Moreover, selection for these traits would promote yield improvement.

In general, the majority of researchers that have either compared or used selection indices in corn have favored the use of indices that are parameter free and/or weight free. The use of any selection index in corn improvement will depend on the goals of the breeding program and also on the interrelationships that may exist among the traits under selection. If the objective is to select those individuals or families with the highest aggregate genotype then, in theory, the Smith-Hazel index would be the best index to use. However, if simultaneous improvement in several traits is desired other alternative indices could be more appropriate than the Smith-Hazel.

The primary objective of recurrent selection is to increase the frequency of favorable alleles for traits of agronomic importance. As the frequency of favorable alleles increases the probability of extracting inbred lines from the

population with the desired characteristics also increases. Corn breeders are generally interested in developing inbred lines that are improved for several traits. For recurrent selection to produce these types of lines, several traits must be improved simultaneously. Selection indices are known to be more efficient than other multiple trait selection methods. The objective of this study is to compare the effectiveness of different selection index methods on the simultaneous improvement of grain yield, grain moisture, root lodging and stalk lodging in corn populations under recurrent selection.

Materials and Methods

The data used to compare selection indices were obtained from the Iowa Stiff Stalk Synthetic (BSSS) corn population. The BSSS was developed in 1933-34 by G. F. Sprague from the following 16 lines: IaI159, IaI224, IaOs420, IaWD456, Ind. 461-3, Ill. 12E, CI617, CI540, Ill. Hy, Oh3167B, Ind. AH83, Ind. Tr9-1-1-6, F_1B1-7-1, A3G-3-1-3, CI187-2 and LE23. They were selected by different corn breeders for having acceptable stalk quality (Hallauer et al., 1983). This population is considered above average as a source of inbred lines that are above average for combining ability with other elite lines. Lines originating from BSSS are used extensively in hybrids in the U.S. corn belt (Hallauer and Miranda, 1988).

Five (out of seven) cycles of half-sib recurrent selection and six cycles of selfed family recurrent selection were used. Two of the seven cycles of selection from the half-sib family recurrent selection program were not considered. Cycle 1 was evaluated at only one location in 1948, resulting in variance-covariance estimates biased due to the genotype x environment interaction effects and cycle 3 had a negative estimate of the genetic component of variance for yield.

For the half-sib family selection program, the number of lines evaluated varied from cycle to cycle, but the number of lines selected was always ten. The evaluation of lines from each cycle was conducted using lattices replicated in two to four environments. For the selfed family selection program, 100 lines were evaluated in cycles 0 to 4 and 150 in cycle 5. Ten lines were selected in cycles 0 and 1 and twenty during each of the remaining cycles. The first three cycles were evaluated using lattice designs and the last three using replications in sets design. In each of the six cycles, the evaluations were conducted in three environments.

The experiments conducted in lattice designs were analyzed as such, except for cycle 2 of the selfed family selection which was analyzed as a randomized complete-block design. Grain yield was adjusted by differences in stand using covariance analysis, this analysis was performed only

for those experiments that were considered as having stand problems when they were originally conducted. To remove the effect of checks on the parameter estimates, combined analyses of variance based on the adjusted family (genotypes) means for each environment obtained from the lattice and covariance analyses were performed. In these analyses, the mean squares for environments, genotypes and the genotype-environment interaction were expressed in a per observation basis to conform with the previous analyses. The experiments conducted using a replications in sets design were analyzed accordingly. For each of the cycles, estimates of phenotypic and genotypic variances and covariances were calculated by equating the expected mean squares to their observed values.

The indices compared for simultaneously improving grain yield, grain moisture, root lodging and stalk lodging were three of the Smith-Hazel type, the corresponding base indices, two indices of the Smith 1981-type when genotypic and phenotypic correlations are assumed to be zero, and two weight-free indices. In order to improve grain moisture, root lodging and stalk lodging they have to be reduced, consequently the relative "economic values" assigned to them must be negative.

The three Smith-Hazel indices differed in their relative "economic values" (a_i).

1) $a_i = T/h_i^2(P_i)^{1/2}$, where T is an arbitrarily assigned

relative importance value, h_i^2 is the heritability estimate on a family mean basis for the i-th trait and P_i is the phenotypic variance of the i-th trait (Young, 1961).

2) $a_i = 1/(P_i)^{1/2}$, where P_i is as above.

3) All traits with equal economic values.

The "economic values" for grain moisture, root lodging and stalk lodging were multiplied by -1 to decrease the values for these traits. The index weights for the Smith-Hazel indices were calculated as follows:

$$\underline{b} = P^{-1}G\underline{a}$$

Where $\underline{b}$ and $\underline{a}$ are the vectors of index weights and relative "economic values" for the traits in the index, respectively; P^{-1} is the inverse of the phenotypic variance-covariance matrix; G is the genotypic variance-covariance matrix.

The resulting index is expressed as:

$$I = b_1X_1 + b_2X_2 + b_3X_3 + b_4X_4$$

Where the b's and the X's are the index weights and the average phenotypic values of grain yield, grain moisture, root lodging and stalk lodging, respectively.

The three base indices (Brim et al., 1959) corresponded to the previous three Smith-Hazel indices. In the case of the base indices, the relative "economic values" are used directly as index weights, resulting in the index,

$$I = a_1X_1 + a_2X_2 + a_3X_3 + a_4X_4.$$

The two Smith 1981-type indices ($b_i = a_i h_i^2$), which are the solutions from the optimum index if the traits were uncorrelated (Hazel, 1943), were calculated using the inverse of the phenotypic standard deviation and equal "economic values".

The multiplicative index (Elston, 1963), also known as Elston weight-free index (EWF), was calculated as

$$I = (X_1 - l_1)(m_2 - X_2)(m_3 - X_3)(m_4 - X_4).$$

Where the Xs are the family mean values for grain yield, grain moisture, root lodging and stalk lodging, respectively; l_1 is the minimum family mean value for grain yield; and the m's are the maximum family mean values for grain moisture, root lodging and stalk lodging, respectively.

The rank summation index (Mulamba and Mock, 1978) was calculated as follows: first all families were ranked from lowest to highest for grain yield, and from highest to lowest for each of the other three traits. Then, the index for each family was calculated by summing the ranks of the four traits.

$$I = \Sigma_{i=1}^{n} R_i.$$

Where, R_i is the rank of the i-th trait.

Single-trait selection for each of the four traits was also performed. The symbols used to refer to each of the indices are shown in Table 1. All indices were estimated in each of the cycles considered.

For each of the indices compared, truncation selection

was practiced on the index values obtained for each of the families evaluated in each cycle of selection. The number of lines selected was ten in each cycle, except for cycles 2 to 5 of the selfed family recurrent selection in which twenty lines were selected. For comparing the different indices, selection differentials were calculated and expressed as a percentage of the selection differential obtained when single-trait selection was practiced. The observed selection differentials for each trait were tested to determine if they were significantly different from zero. A t-test at the 0.05 probability level was calculated as follows:

$$t = SD/\{(GxE\ MS/er)(1/n_s - 1/n)\}^{1/2}$$

Where SD is the selection differential; GxE MS is the genotype-environment interaction mean square from the combined analysis of variance for each cycle; e is the number of environments; and r is the number of replications used to evaluate the families; n_s is the number of families selected and n is the number of families evaluated in each cycle (T. B. Bailey, Department of Statistics, Iowa State University, personal communication, 1989).

Predicted genetic gains were calculated for all indices, except RSI and EWF, for which a procedure is not available. The formula used was the following:

$$\underline{D} = kG\underline{b}/(\underline{b}'P\underline{b})^{1/2} \quad \text{(Lin, 1978)}$$

where k is the standardized selection differential; G and P

are the genetic and phenotypic variance-covariance matrices, respectively; and $\underline{b}$ is the vector of index weights. For single-trait selection, the $\underline{b}$ vector consisted of 1 for the trait under selection and 0 for the other three traits. These predicted genetic gains were expressed in genetic standard deviation units by dividing the predicted gain for a trait by its genetic standard deviation.

For determining similarities among indices, rank correlations were calculated for all pairs of indices and between all indices and yield. These correlations were calculated by using the rankings obtained with each of the indices for all the lines evaluated in each cycle. Percentage of selected lines in common were also computed for the same purpose.

Table 1. Symbols and description of the selection indices compared

Symbol	Index
SHY	Smith-Hazel using Young's economic values.
SHSD	Smith-Hazel using the inverse of the phenotypic standard deviation as economic values.
SHE	Smith-Hazel using equal economic values.
BY	Base corresponding to the SHY.
BSD	Base corresponding to the SHSD.
BE	Base corresponding to the SHE.

Table 1. (continued)

Symbol	Index
SSD	Smith 1981-type using the inverse of the phenotypic standard deviation as economic values.
SE	Smith 1981-type using equal economic values.
EWF	Elston weight-free (multiplicative).
RSI	Rank summation.
YLD	Grain yield per se (q/ha at 15.5 % moisture).
MOIST	Percentage grain moisture per se.
RTLDG	Percentage root lodging per se.
SKLDG	Percentage stalk lodging per se.

Results and Discussion

For both recurrent selection schemes, the estimates of heritability (h^2) were highest for grain moisture, followed by grain yield, stalk lodging and root lodging (Table 2). These estimates were higher, and in general, less variable in the selfed family selection (SFS) than in the half-sib family selection (HSFS). The differences in heritability estimates between the two selection schemes is a reflection of the differences in genetic variances observed between them.

Variation in heritability estimates were observed from cycle to cycle.

There were variations in the phenotypic and genotypic correlations across cycles for both recurrent selection schemes. On the average, the phenotypic correlations were smaller than the corresponding genotypic correlations. All correlations were low ($|r| < .3$); but, for individuals cycles, there were several correlations with absolute values higher than .3 (Table 2). The correlation estimates changed in a random fashion with regard to sign and size across cycles (data not shown). This variation in the correlation estimates could simply be due to estimation errors, and possibly all values could be estimates of a common value close to zero. These changes in the structure of the correlations could affect the performance of the different selection indices under study.

In cycle 4 of half-sib family selection (data not shown), root lodging was unfavorably correlated (genotypically and phenotypically) with yield and stalk lodging; all other traits were favorably correlated except for moisture and root lodging which had a correlation near zero. In this specific cycle, the selection differentials were in the desired direction for grain yield, grain moisture and stalk lodging for all selection indices being compared. In the case of root lodging, the three Smith-Hazel (SHY, SHSD, SHE) and the two

Table 2. Estimates of genetic variances (σ_g^2), heritabilities (h^2), and phenotypic (r_{ph}) and genotypic correlations (r_g) for grain yield, grain moisture, root lodging and stalk lodging of the Iowa Stiff Stalk Synthetic under half sib family selection and selfed family selection

Trait		HALF-SIB FAMILY SELECTION	
		Average[a]	Range
Yield (Y)	σ_g^2	7.37	3.70, 10.65
	h^2	0.49	0.17, 0.69
Moisture (M)	σ_g^2	1.06	0.62, 1.71
	h^2	0.69	0.56, 0.78
Root lodging (R)	σ_g^2	8.54	1.93, 31.06
	h^2	0.32	0.05, 0.52
Stalk lodging (S)	σ_g^2	22.41	0.56, 50.27
	h^2	0.48	0.05, 0.75
YM	r_{ph}	-0.06	-0.22, 0.29
	r_g	0.10	-0.19, 0.46
YR	r_{ph}	0.02	-0.19, 0.24
	r_g	-0.09	-0.65, 0.34
YS	r_{ph}	-0.07	-0.17, 0.07
	r_g	-0.14	-0.33, 0.06
MR	r_{ph}	-0.02	-0.05, 0.04
	r_g	-0.10	-0.24, 0.01
MS	r_{ph}	0.004	-0.25, 0.32
	r_g	-0.21	-1.03, 0.40
RS	r_{ph}	-0.06	-0.21, 0.16
	r_g	0.04	-0.38, 0.58

[a]Average and range over five and six cycles of half sib and selfed family selection, respectively.

SELFED FAMILY SELECTION	
Average	Range
49.75	27.87, 80.79
0.66	0.51, 0.81
3.79	1.71, 7.88
0.78	0.66, 0.87
52.82	1.17, 175.40
0.46	0.15, 0.66
26.45	0.67, 55.67
0.49	0.20, 0.72
0.09	-0.33, 0.45
0.12	-0.35, 0.44
0.02	-0.09, 0.09
0.08	-0.05, 0.30
0.07	0.01, 0.16
0.21	-0.02, 0.35
0.07	-0.02, 0.16
0.13	-0.04, 0.22
-0.04	-0.27, 0.11
-0.06	-0.53, 0.24
0.10	-0.06, 0.30
0.27	-0.06, 0.52

Smith (SSD, SE) indices produced selection differentials in the undesired direction. The BSD and BE indices produced small selection differentials in the desired direction. For the remaining indices (BY, EWF and RSI), there was more harmony in their responses. All of them gave selection differentials (expressed as a percentage of the single-trait selection differentials) higher than 40 for the four traits. The unfavorable responses for root lodging observed in some of the indices can be attributed to the unfavorable correlations mentioned above, some indices being less affected by the size and magnitude of the correlations among traits.

In cycle 5 of selfed family selection, only yield and moisture were unfavorably correlated, all other correlations between traits were either favorable or very low. In this cycle, most of the selection indices produced selection differentials in the desired direction for the four traits, except for SHE, BE and SE in which selection differentials in the undesired direction were obtained for grain moisture.

Averages and ranges of selection differentials, expressed as a percentage of the selection differentials obtained by single-trait selection, for the four traits and the selection indices considered are presented in Table 3. The three Smith-Hazel indices (SHY, SHSD, SHE) produced, on the average, selection differentials lower than 40 for some of the traits. It was also observed in some instances for these three

Table 3. Selection differentials for grain yield, grain moisture, root lodging and stalk lodging for various selection indices expressed as a percentage of the single-trait selection differential

	HALF-SIB FAMILY SELECTION			
Index	Grain yield	Grain moisture	Root lodging	Stalk lodging
SHY	51.9[a] 36.3, 84.5	16.8 -83.1, 74.3	36.0 -16.7, 93.3	61.5 0.0, 87.6
SHSD	52.6 36.3, 79.7	59.9 32.4, 84.3	33.9 -13.7, 92.0	49.5 -21.5, 76.9
SHE	55.2 -8.4, 97.1	10.4 -23.0, 45.9	33.3 -33.2, 86.6	64.3 -16.5, 97.8
BY	43.3 13.9, 94.6	35.4 13.6, 58.7	67.1 54.5, 75.4	60.7 41.7, 80.8
BSD	66.2 35.8, 88.4	58.1 33.1, 78.2	44.5 7.4, 77.2	51.5 31.0, 63.6
BE	60.9 7.7, 84.5	23.0 4.3, 35.8	62.4 20.9, 93.3	65.2 42.9, 78.9
SSD	59.1 35.8, 89.0	61.2 43.2, 78.2	36.1 -16.7, 85.7	51.2 2.5, 87.3
SE	60.3 7.7, 96.6	32.7 6.5, 55.8	43.7 -33.2, 90.6	63.6 19.8, 97.8
EWF	58.4 26.9, 88.4	54.6 42.7, 74.4	54.1 42.3, 77.2	52.5 36.0, 58.5
RSI	59.0 38.5, 78.3	47.4 33.1, 67.0	62.2 45.5, 94.6	54.2 36.9, 70.3

[a]Mean (first line) and range (second line) over five cycles of half sib family selection and six cycles of selfed family selection.

SELFED FAMILY SELECTION

Grain yield	Grain moisture	Root lodging	Stalk lodging
24.2	63.6	73.2	58.2
-3.9, 69.6	39.8, 89.3	50.1, 86.1	43.7, 79.1
42.0	63.7	62.2	48.7
12.5, 69.7	53.8, 71.0	45.7, 85.1	13.9, 83.2
69.0	16.5	56.1	31.4
40.3, 93.3	-20.6, 46.1	24.4, 73.0	-54.5, 73.6
37.0	43.3	73.4	61.5
-6.1, 69.6	27.1, 60.6	48.2, 99.9	15.2, 88.7
45.4	57.2	68.4	51.6
28.2, 72.2	47.0, 68.5	55.6, 86.1	43.7, 62.4
62.4	17.6	65.5	30.1
25.2, 85.5	-24.6, 35.0	23.7, 85.2	-19.7, 70.2
50.3	63.2	53.5	39.8
26.4, 80.6	53.8, 71.2	19.2, 85.4	-5.3, 83.2
72.2	19.5	55.9	25.8
58.5, 90.9	-24.6, 46.9	15.4, 84.6	-33.8, 67.4
53.8	56.0	58.6	54.3
43.7, 63.5	36.9, 65.0	31.4, 79.4	29.6, 87.8
39.4	50.5	71.3	57.0
16.1, 66.7	35.7, 62.3	53.6, 88.6	31.5, 75.4

Table 3. (continued)

	HALF-SIB FAMILY SELECTION			
Index	Grain yield	Grain moisture	Root lodging	Stalk lodging
YLD	100.0	12.4 -34.5, 39.3	0.3 -52.8, 46.0	17.1 -8.0, 37.8
MOIST	-4.8 -60.8, 19.7	100.0	-3.0 -26.5, 26.8	-4.5 -25.0, 21.6
RTLDG	0.3 -17.1, 26.2	10.9 -4.3, 30.7	100.0	2.9 -36.2, 54.4
SKLDG	9.2 -15.4, 32.0	14.3 -26.4, 43.5	-8.4 -38.6, 71.4	100.0

SELFED FAMILY SELECTION			
Grain yield	Grain moisture	Root lodging	Stalk lodging
100.0	-17.1 -52.8, 14.2	3.8 -32.1, 37.9	-26.5 -95.8, 10.7
-20.0 -58.9, 7.7	100.0	12.8 -0.7, 36.9	-2.3 -36.4, 30.7
-9.2 -26.1, 27.5	14.1 -10.9, 39.2	100.0	3.5 -34.4, 39.4
-6.2 -41.0, 75.9	2.1 -13.2, 18.7	8.8 -8.9, 34.0	100.0

indices, that very low and even selection differentials in the undesired direction were obtained for both recurrent selection schemes indicating that they were affected by the correlation structure among the traits. Similar results were obtained for SSD, SE, BY and BE. The index BSD gave, on the average, relatively large selection differentials except for one cycle in which the selection differential obtained for root lodging was very low (7.4) in the HSFS. Selection differentials in the undesired direction were not observed with this selection index.

The EWF gave average selection differentials higher than 50 for all traits and for both recurrent selection schemes. The RSI performed similarly to the EWF, but gave lower selection differentials for grain yield in the SFS. Neither EWF nor RSI produced selection differentials that were in the undesired direction.

As expected, single-trait selection differentials were highest for the specific trait under selection. Low favorable correlated responses or more frequently unfavorable correlated responses were observed when the trait under selection was unfavorably correlated with any of the other traits.

The number of cycles in which significant (favorably or unfavorably different from zero) selection differentials were obtained for each selection index for both selection schemes are presented in Table 4. The RSI, EWF and BSD gave the

Table 4. Number of cycles in which selection differentials were favorably (F) or unfavorably (U) different from zero (p = 0.05) for grain yield, grain moisture, root lodging and stalk lodging

	Grain Yield		Grain moisture		Root lodging		Stalk lodging	
Index	F	U	F	U	F	U	F	U
SHY	5	0	4	1	3	0	4	0
	3	0	6	0	6	0	5	0
SHSD	5	0	5	0	3	0	4	0
	6	0	6	0	6	0	3	0
SHE	4	0	3	2	2	1	4	0
	6	0	3	1	5	0	4	1
BY	4	0	4	0	5	0	5	0
	5	0	6	0	6	0	5	0
BSD	5	0	5	0	4	0	5	0
	6	0	6	0	6	0	5	0
BE	4	0	4	0	4	0	5	0
	6	0	5	1	5	0	4	0
SSD	5	0	5	0	3	0	4	0
	6	0	6	0	5	0	4	0
SE	4	0	4	0	4	1	4	0
	6	0	4	1	5	0	4	0
EWF	5	0	5	0	5	0	5	0
	6	0	6	0	5	0	5	0
RSI	5	0	5	0	5	0	5	0
	6	0	6	0	6	0	5	0

[a]Five cycles of half-sib family selection (first line) and six cycles of selfed family selection (second line). the selection differentials.

highest number of cycles in which the selection differentials were significant in the favorable direction for all traits. The EWF and BSD resulted in one cycle with no significant selection differentials for root lodging and stalk lodging. The RSI resulted in only one cycle with no significant response for stalk lodging. Selection differentials in the unfavorable direction were not observed for RSI, EWF and BSD.

All the other selection indices evaluated had a lower number of cycles with significantly selection differentials in the desired direction. The SHE, SE and BE indices even gave significant selection differentials in the undesired direction for some of the traits. Selection differentials in the undesired direction for grain yield were not found for any of the selection indices.

Predicted genetic gains in genotypic standard deviation units for all selection indices, except EWF and RSI, are shown in Table 5. The predicted gains were in close agreement with the selection differentials. High or low selection differentials were generally associated with correspondingly high or low predicted genetic gains. The BSD index showed more uniform predicted genetic gains than the other indices. This index consistently gave favorable responses for all traits in both recurrent selection schemes, except for one cycle of the HSFS where unfavorable genetic change was predicted for stalk lodging. The predicted genetic gains

Table 5. Predicted genetic gains for grain yield, grain moisture, root lodging and stalk lodging for various selection indices expressed as genetic standard deviations

	HALF-SIB FAMILY SELECTION			
Index	Grain yield	Grain moisture	Root lodging	Stalk lodging
SHY	0.54[a] 0.17, 0.93	-0.09 -1.11, 0.95	-0.67 -1.08,-0.07	-1.07 -1.23,-0.91
SHSD	0.58 0.38, 1.12	-0.70 -1.17,-0.05	-0.42 -0.93, 0.06	-0.63 -1.28, 0.72
SHE	0.76 0.07, 1.28	-0.01 -0.78, 0.78	-0.47 -0.87, 0.11	-0.95 -1.45,-0.05
BY	0.44 0.18, 0.79	-0.24 -0.89, 0.29	-0.52 -0.82,-0.24	-0.60 -0.87,-0.09
BSD	0.57 0.35, 0.88	-0.60 -1.00,-0.18	-0.43 -0.81,-0.09	-0.52 -1.05, 0.60
BE	0.63 0.13, 0.87	-0.11 -0.69, 0.38	-0.48 -0.70,-0.02	-0.80 -1.34, 0.20
SSD	0.55 0.33, 0.93	-0.87 -1.14,-0.42	-0.26 -0.70, 0.05	-0.42 -1.20, 1.04
SE	0.72 0.18, 1.19	-0.26 -0.72, 0.34	-0.35 -0.60, 0.12	-0.77 -1.44, 0.53
YLD	1.26 0.81, 1.75	-0.14 -0.57, 0.36	-0.27 -1.23, 0.62	-0.13 -0.32, 0.08

[a]Mean (first line) and range (second line) over five cycles of half sib family selection and six cycles of selfed family selection.

SELFED FAMILY SELECTION

Grain yield	Grain moisture	Root lodging	Stalk lodging
0.20 -0.21, 0.50	-0.69 -1.34,-0.31	-0.77 -1.10,-0.49	-0.63 -0.90,-0.32
0.37 -0.18, 1.08	-0.85 -1.35,-0.56	-0.66 -0.96,-0.40	-0.41 -0.81, 0.12
0.64 0.20, 1.19	-0.19 -0.75, 0.05	-0.67 -1.14,-0.30	-0.47 -0.92, 0.28
0.23 0.03, 0.50	-0.41 -0.60,-0.19	-0.71 -0.90,-0.41	-0.60 -0.71,-0.40
0.42 0.06, 0.91	-0.66 -1.09,-0.46	-0.70 -0.91,-0.56	-0.48 -0.75,-0.14
0.60 0.30, 0.90	-0.15 -0.55, 0.12	-0.71 -1.12,-0.32	-0.44 -0.81, 0.14
0.48 0.08, 1.19	-0.83 -1.27,-0.52	-0.60 -0.84,-0.38	-0.34 -0.80, 0.18
0.71 0.39, 1.19	-0.21 -0.74, 0.07	-0.63 -1.10,-0.22	-0.40 -0.90, 0.27
1.25 0.99, 1.56	0.13 -0.54, 0.54	0.10 -0.08, 0.34	0.28 -0.03, 0.55

Table 5. (continued)

	HALF-SIB FAMILY SELECTION			
Index	Grain yield	Grain moisture	Root lodging	Stalk lodging
MOIST	0.06 -0.65, 0.39	-1.70 -2.73,-1.44	0.17 -0.01, 0.36	0.33 -0.57, 1.49
RTLDG	0.03 -0.57, 0.57	0.07 -0.01, 0.14	-1.83 -5.32,-0.38	0.15 -0.19, 0.61
SKLDG	0.18 -0.08, 0.48	0.09 -0.58, 0.59	0.26 -0.23, 1.15	-1.50 -2.81, -0.39

SELFED FAMILY SELECTION			
Grain yield	Grain moisture	Root lodging	Stalk lodging
-0.14 -0.61, 0.56	-1.36 -1.61,-1.13	-0.17 -0.27, 0.07	0.06 -0.39, 0.60
-0.09 -0.31, 0.06	-0.12 -0.22, 0.05	-1.03 -1.41,-0.54	-0.23 -0.53, 0.07
-0.21 -0.39, 0.03	0.05 -0.19, 0.42	-0.28 -0.57, 0.07	-1.05 -1.36,-0.78

calculated for BSD were used to approximate the predicted gains for EWF and RSI. Baker (1974) showed that EWF could be closely approximated by the BSD index, and Crosbie et al. (1980) found that RSI could be approximated by BSD because both indices transform the data so that the variances for each trait are equal. Therefore, the genetic gains predicted for the BSD index are also applicable for EWF and RSI.

These results suggest that the EWF, BSD and RSI could be used for the simultaneous improvement of grain yield, grain moisture, root lodging and stalk lodging in corn. These results closely agree with the results obtained by Crosbie et al. (1980). They compared several selection indices to improve cold tolerance in corn and concluded that the use of BSD, RSI and EWF indices should be considered for the improvement of composite traits, such as cold tolerance. And as they indicated, these three selection indices combine 1) simplicity of use; 2) freedom from need to estimate genetic parameters; and 3) good selection differentials.

Reports on the use of the multiplicative and rank summation index for the simultaneous improvement of several traits have appeared in the literature. The multiplicative index has been successfully used by the University of Nebraska corn breeding project since 1968 for the simultaneous improvement of grain yield, plant lodging and dropped ears in corn (West et al., 1980; Compton and Lonnquist, 1982; Odhiambo

and Compton, 1989). Mulamba and Mock (1978) reported that selection for leaf orientation rating, leaf area per plant, and pollen shed to silking interval, using the RSI would change these traits in the desired direction.

The SHE, BE and SE indices were previously compared by Smith et al. (1981a) for the improvement of grain yield, grain moisture, root lodging, and stalk lodging. They found that the SE index resulted in little predicted loss of efficiency while insuring that selection for the individual traits was in the desired direction. In my study, selection differentials for SE were on the average in the desired direction, but were generally not as large as the selection differentials obtained for the indices BSD, RSI and EWF. Also, in several cycles low and even selection differentials in the undesired direction were observed for some of the traits when selections were made on SE.

In general, rank correlations between indices were higher in the SFS than in the HSFS (Table 6). Generally for both recurrent selection methods, high rank correlations ($r > .90$ on the average) were found between indices that were somewhat related. The indices SHSD, BSD and SSD were highly correlated with each other. The high correlations among these indices were expected because they have the same relative "economic values". A similar pattern was observed for the SHE, BE and SE indices which also share the same relative "economic

Table 6. Rank correlations among various selection indices in half sib family selection (above diagonal) and selfed family selection (below diagonal)[a]

Index	SHY	SHSD	SHE	BY	BSD
SHY		.76[b] .17, .99	.80 .61, .92	.72 .13, .98	.73 .06, .99
SHSD	.94 .87, .99		.82 .67, .93	.64 .04, .96	.88 .68, .98
SHE	.81 .69, .87	.81 .72, .87		.56 .15, .84	.71 .61, .83
BY	.90 .74, .99	.80 .56, .98	.74 .49, .91		.89 .70, .99
BSD	.96 .91, .99	.95 .92, .99	.85 .82, .87	.92 .79, .99	
BE	.81 .71, .84	.77 .74, .79	.97 .90, .99	.80 .58, .91	.85 .78, .92
SSD	.91 .82, .99	.98 .97, .99	.81 .70, .89	.79 .55, .97	.96 .93, .99
SE	.79 .68, .87	.81 .75, .86	.98 .93, .99	.74 .50, .91	.86 .78, .89
EWF	.89 .81, .96	.91 .86, .96	.80 .72, .86	.83 .58, .96	.94 .90, .97
RSI	.90 .82, .97	.89 .81, .95	.76 .66, .84	.86 .74, .97	.91 .84, .97
YLD	.24 .03, .45	.35 .06, .60	.58 .35, .80	.31 .21, .42	.42 .28, .56

[a]Correlation coefficients whose absolute values are more than .20 are significant at the .05 level of probability.

[b]Mean (first line) and range (second line) over five cycles of half sib family selection and six cycles of selfed family selection.

BE	SSD	SE	EWF	RSI	YLD
.75 .25, .93	.63 -.12, .99	.71 .27, .91	.64 .04, .94	.72 .04, .96	.39 .27, .59
.78 .55, .90	.95 .92, .99	.88 .78, .94	.80 .66, .92	.87 .70, .95	.43 .23, .86
.87 .61, .99	.71 .54, .90	.95 .90, .99	.62 .43, .86	.71 .61, .84	.48 .03, .99
.84 .81, .86	.68 .21, .97	.63 .31, .86	.84 .63, .94	.85 .67, .94	.46 .22, .89
.88 .82, .91	.92 .82, .99	.83 .80, .85	.94 .91, .97	.96 .95, .98	.53 .40, .67
	.77 .61, .90	.92 .74, .99	.81 .69, .88	.86 .78, .90	.50 .08, .74
.78 .74, .81		.85 .78, .90	.86 .82, .92	.90 .83, .96	.47 .36, .70
.97 .93, .99	.83 .77, .89		.75 .61, .88	.82 .78, .84	.52 .12, .92
.82 .78, .89	.93 .89, .96	.83 .79, .86		.86 .81, .90	.46 .24, .73
.76 .69, .84	.88 .82, .94	.76 .69, .83	.82 .75, .90		.52 .41, .67
.56 .44, .71	.43 .24, .66	.63 .46, .82	.45 .34, .54	.34 .18, .52	

values".

The BSD was highly correlated with the EWF and RSI, but the correlation between EWF and RSI was relatively smaller. Similar results were reported by Crosbie et al. (1980) for these indices, except that they found a higher correlation ($r = .96$) between EWF and RSI than the one found in this study ($r = .84$).

The lowest rank correlations observed were between YLD and all the other indices. This was expected because the indices were selecting for other traits in addition to grain yield. When single-trait selection is practiced, the ranking of the genotypes is based exclusively on that trait. With index selection, the ranking is based on the index values which are a linear combination of all the traits being considered in the index; consequently, in the case of low and/or unfavorable correlations among traits, the highest ranked genotypes based on the index will not always be the highest for any of the traits included in the index. This will result in low correlations between genotypes ranked using index selection and single-trait selection.

In general, percentages of selected lines in common between indices were higher in the SFS than in the HFFS (Table 7). Close agreement was found between the rank correlations and the percent of selected families in common for the various selection indices. As the rank correlations between indices

Table 7. Percent of selected families in common for various selection indices in half-sib family selection (above diagonal) and selfed family selection (below diagonal)

Index	SHY	SHSD	SHE	BY	BSD
SHY		68[a] 0, 100	58 30, 80	64 10, 90	64 0, 90
SHSD	82 50, 100		58 50, 80	54 10, 80	76 60, 90
SHE	57 30, 75	62 50, 75		38 0, 60	50 40, 60
BY	78 50, 100	73 40, 90	59 40, 85		68 40, 80
BSD	83 50, 100	85 70, 95	65 50, 80	83 60, 95	
BE	56 30, 70	58 45, 70	82 65, 95	62 50, 80	65 50, 75
SSD	74 40, 95	89 80, 100	65 50, 80	68 40, 85	82 70, 95
SE	56 30, 70	62 50, 70	90 80, 95	60 45, 75	65 50, 75
EWF	63 45, 80	72 50, 80	56 35, 70	61 20, 80	71 35, 90
RSI	73 30, 90	77 65, 95	61 50, 80	82 65, 95	85 75, 95
YLD	24 0, 50	32 20, 60	56 35, 75	32 15, 50	35 25, 55

[a]Mean (first line) and range (second line) over five cycles of half sib family selection and six cycles of selfed family selection.

BE	SSD	SE	EWF	RSI	YLD
64 20, 100	64 0, 100	60 10, 90	58 0, 80	62 0, 90	32 20, 60
58 30, 70	88 80, 90	70 60, 80	70 60, 80	72 50, 90	34 20, 50
64 30, 90	54 40, 80	78 60, 100	46 30, 50	48 30, 60	42 0, 80
72 60, 90	56 20, 80	52 20, 80	74 40, 90	78 50, 90	28 10, 70
70 50, 80	82 70, 100	66 50, 80	88 80, 100	88 70, 100	46 20, 60
	60 40, 70	80 60, 100	72 60, 80	78 60, 90	36 0, 60
59 45, 70		72 50, 80	76 70, 90	76 60, 90	36 20, 60
84 70, 95	67 50, 80		64 50, 70	64 40, 80	42 0, 80
51 20, 65	71 50, 85	56 30, 70		86 80, 90	36 10, 60
62 40, 75	71 60, 90	62 50, 70	64 35, 80		38 20, 50
51 35, 65	38 20, 55	55 40, 75	36 30, 55	32 20, 50	

were higher, there was also a tendency for the percent of selected families in common to be higher.

The indices SHSD, BSD and SSD selected, on the average of the two selection schemes, more than 80% of families in common. For these indices, as the rank correlations were higher the percentages of selected families in common were also higher. Similar patterns of association were observed between rank correlations and percentages of selected families in common for the SHE, BE and SE indices, and for the BSD, EWF and RSI. The percentage of selected families in common between BSD and EWF and BSD and RSI was higher than 78%. The percentage of selected families in common between RSI and EWF, however, was only 74%. Even though the RSI and EWF gave, on the average, relatively similar selection differentials, they selected different genotypes. This is observed in the relatively low rank correlations (Table 6) and also in the percentage of selected families in common (Table 7) obtained with these two indices.

From the results of this study, it can be concluded that the degree of improvement on each of the traits is influenced by the structure of the correlations between traits. In general, the selection indices most influenced by these correlations were the SHY, SHSD, SHE, SSD, SE, BY and BE. The BSD, EWF and RSI were less affected by the correlation structure resulting in a more even improvement for the four

traits considered. The use of these three indices should seriously be considered when simultaneous improvement of several traits is desired. Besides the efficiency shown in this study, these three indices are simple to use and they do not require the estimation of genetic parameters, BSD only requires the estimation of the phenotypic standard deviation. For the EWF and RSI, neither genetic parameter estimates nor relative "economic weights" are needed. But, if desired some importance weights can be assigned to them. For the RSI, the ranks for each trait can be multiplied by the specific weight desired; and in the case of the EWF, the traits can be weighted by changing accordingly the value that is subtracted from each of the traits.

Establishing which of these three indices should be used for the simultaneous selection of grain yield, grain moisture, root lodging, and stalk lodging in corn would be difficult. Apparently any of them could be used and each of them would produce, on the average, similar results. Due to the ease in the implementation of these three indices, and the computational facilities available now, it would be advisable to apply all of them in each cycle of selection and decide after selection differentials have been obtained for each index. And definitely, as St. Martin et al. (1982) and Smith et al. (1981b) suggested, the breeder has to make the final selections based on his experience and/or judgement, the

results obtained with the selection indices will be only an aid for making that final decision.

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SECTION II. EFFECT OF POOLING VARIANCES AND COVARIANCES OVER SEVERAL CYCLES OF SELECTION ON THE ESTIMATION OF A SELECTION INDEX

Abstract

Interest in use of the selection indices proposed by Smith (1936) and Hazel (1943) has increased because the objective of most breeding programs is the simultaneous improvement of several traits. Estimates of phenotypic and genotypic parameters are required for the computation of a Smith-Hazel selection index. Sampling errors on the estimation of the parameters needed to develop an estimated index could cause it to be less effective than expected.

Several researchers have suggested the pooling of information from different cycles of selection as a method of improving parameter estimates. The objective of this study was to evaluate the effect of pooling phenotypic and genotypic variances and covariances over several cycles of selection on the estimation of a selection index for improving grain yield, grain moisture, root lodging and stalk lodging in corn. Three Smith-Hazel selection indices that differed only in the relative economic values (a_i) assigned to the four traits were studied.

The phenotypic and genotypic variances and covariances

were estimated for each of the cycles considered. The selection indices were calculated by using the parameter estimates from a single cycle of selection or by pooling the parameter estimates of a single cycle with one to four of the previous cycles.

Selection was practiced in three cycles of half-sib family selection and in four cycles of selfed family selection. Selection differentials, expressed as a percentage of the selection differentials obtained with single trait selection, and predicted genetic gains were calculated for each selection index in each cycle of selection.

In general, the Smith-Hazel selection indices calculated by pooling parameter estimates were neither better for improving the four traits simultaneously nor for improving the aggregate genotype than the selection indices calculated using data of the particular cycle in which selection was being practiced.

Introduction

When recurrent selection is used in a breeding program, simultaneous selection for several traits is necessary. Interest in use of the selection indices proposed by Smith (1936) and Hazel (1943) (Smith-Hazel index), has increased because the objective of most breeding programs is the

simultaneous improvement of several traits (Hallauer and Miranda, 1988).

The selection index is a linear combination of phenotypic values weighted in such a way that the expected gain in the aggregate genotype is maximized. The selection index and the aggregate genotype are defined as (Lin, 1978):

$$\text{Index:} \quad I = \Sigma_{i=1}^{n} b_i x_i$$

$$\text{Aggregate genotype:} \quad H = \Sigma_{i=1}^{n} a_i g_i$$

where n is the number of traits in the index; x_i is the observed phenotypic value of the i-th trait; b_i is the weight assigned to the i-th trait in the selection index; g_i is the unobservable genotypic value of the i-th trait; and a_i is the relative economic value of the i-th trait.

The objective of an index is to find the set of index weights that maximize the correlation between the aggregate genotype and the resulting selection index value. This correlation is maximized by solving the index equations $P\underline{b}=G\underline{a}$. The solution of these equations is given by $\underline{b} = P^{-1}G\underline{a}$. Where $\underline{b}$ and $\underline{a}$ are the vectors of index weights and economic values, respectively, and P and G are the phenotypic and genotypic variance-covariance matrices, respectively.

Phenotypic and genotypic parameters are required for the computation of a selection index. The parameters themselves are not known and estimates are used in index construction. Sampling errors on the estimation of these parameters and the

effect of these errors on the accuracy of the selection index has either motivated the development of other indices in which these parameter estimates are not needed (Brim et al., 1959; Elston, 1963; Mulamba and Mock, 1978) or suggestions of how these parameter estimates can be improved (Brim et al., 1959; Hallauer and Miranda, 1988; Kauffman and Dudley, 1979; Suwantaradon et al., 1975).

The effects of errors of parameter estimation on the efficiency of selection indices have been investigated. Heidhues (1961) investigated the effect of errors of parameter estimation on the accuracy of a selection index method. He concluded that if the estimates of the phenotypic and genotypic variances and covariances exceeded theoretically determined limits, then they should be modified to increase the accuracy of the index. Williams (1962) called the index obtained by using sample estimates an estimated index and concluded that errors in the estimation of the parameters needed to develop an estimated index could cause it to be less effective than expected. He also indicated that if the parameter estimates deviate only slightly from their true values, then the use of the estimated index is advisable when it provides a worthwhile improvement over other alternative indices.

Harris (1961) indicated that the inaccuracies of estimation result in indices which will yield progress

somewhat less than the maximum attainable progress. Also the errors of parameter estimation result in inaccuracies in the estimation of progress from selection on a particular estimated index.

In general, actual responses to estimated indices will always be less than response to the optimum index (Baker, 1986). The differences in response between the optimum and estimated indices will be reduced as the differences between parameter estimates and the true parameters are reduced. Some researchers (Brim et al., 1959; Hallauer and Miranda, 1988; Kauffman and Dudley, 1979; Suwantaradon et al., 1975) have suggested that parameter estimates could be improved by pooling information from different cycles of recurrent selection, as compared to using the data pertaining to the specific cycle of selection.

Averaging estimates from different cycles would reduce the sampling error, but if the true values change with selection, the averages would represent biased estimates for each cycle. If the reduction in sampling error offsets the bias introduced by pooling, then it would be worthwhile to pool the parameter estimates and use an index calculated from pooled parameter estimates. In this case, parameter estimates from a new cycle would be pooled with those from previous cycles (Brim et al., 1959). Suwantaradon et al. (1975) suggested that pooling data over three to four cycles of

selection should minimize sampling errors and provide an appropriate index for a particular cycle of selection. In a study conducted by Kauffman and Dudley (1979), selection indices were estimated by pooling estimates from two years. They argued that the combined parameter estimates should be more accurate than those obtained from a single year's data since the change in the true values of these parameters was expected to be small after only a single cycle of selection.

Drawbacks from this approach have been also anticipated. Manning (1956) has argued that using data from the particular cycle of selection may be more effective because the weighting of several traits in an index is a function of the exact environmental conditions in which the crop was grown. Also, Hallauer and Miranda (1988) stated that if significant changes in gene frequency are suspected then estimates from the most recent cycle of selection should be used.

The objective of this study is to evaluate the effect of pooling phenotypic and genotypic variances and covariances over several cycles of selection, as compared to using data from the particular cycle of selection, on the estimation of selection indices for improving grain yield, grain moisture, root lodging and stalk lodging in corn.

Materials and Methods

The data used in this study were obtained from the Iowa Stiff Stalk Synthetic (BSSS) corn population. The BSSS population was developed in 1933-34 by G. F. Sprague from the following 16 lines: IaI159, IaI224, IaOs420, IaWD456, Ind. 461-3, Ill. 12E, CI617, CI540, Ill. Hy, Oh3167B, Ind. AH83, Ind. Tr9-1-1-6, F_1B1-7-1, A3G-3-1-3, CI187-2 and LE23. They were selected by different corn breeders for having acceptable stalk quality (Hallauer et al., 1983). This population is considered above average as a source of inbred lines that are above average for combining ability with other elite lines. Lines originating from BSSS are used extensively in hybrids in the U.S. corn belt (Hallauer and Miranda, 1988).

The data reanalyzed in this study were obtained from five (out of seven) cycles of half-sib and from six cycles of selfed family recurrent selection in the BSSS. Two cycles of selection from the half-sib family recurrent selection program were not used in this study. Cycle 1 was evaluated at only one location in 1948, resulting in variance-covariance estimates biased due to the genotype x environment interaction effects. Cycle 0 was not used because parameter estimates were always pooled over consecutive cycles of selection.

For the half-sib family selection program, the number of lines evaluated varied from cycle to cycle, but the number of

lines selected was always ten. The evaluation of lines from each cycle was conducted using lattices replicated in two to four environments. For the selfed family selection program, 100 lines were evaluated in cycles 0 to 4 and 150 in cycle 5. Ten lines were selected in cycles 0 and 1 and twenty during each of the remaining cycles. The first three cycles were evaluated using lattice designs and the last three using replications in sets design. In each of the six cycles, the evaluations were conducted in three environments.

The experiments conducted in lattice designs were analyzed as such, except for cycle 2 of the selfed family selection which was analyzed as a randomized complete-block design, because there was no gain in efficiency from using the lattice analysis. Grain yield was adjusted for differences in stand using covariance analysis, only when covariance analysis was used in the original analysis of the experiments. To remove the effect of checks on the parameter estimates, combined analyses of variance based on the adjusted family (genotypes) means for each environment obtained from the lattice and covariance analyses were performed. In these analyses, the mean squares for environments, genotypes and the genotype-environment interaction were expressed on a per observation basis to conform with the previous analyses. The experiments conducted using replications in sets design were analyzed accordingly. For each of the cycles, estimates of

phenotypic and genotypic variances and covariances were estimated by equating the expected mean squares to their observed values.

The study was conducted using three Smith-Hazel selection indices that differed only in the relative "economic values" (a_i) assigned to the four traits.

1) $a_i = T/h_i^2(P_i)^{1/2}$, where T is an arbitrarily assigned relative importance value, h_i^2 is the heritability estimate on a family mean basis for the i-th trait and P_i the phenotypic variance of the i-th trait (SHY) (Young, 1961).

2) $a_i = 1/(P_i)^{1/2}$, where P_i is as above (SHSD).

3) All traits with equal economic values (SHE).

The "economic values" for grain moisture, root lodging and stalk lodging were multiplied by -1 because in order to improve them their values have to be reduced. The index weights for the three indices were calculated as follows:

$$\underline{b} = P^{-1}G\underline{a}$$

Where $\underline{b}$ and $\underline{a}$ are the vectors of index weights and relative "economic values" for the traits in the index, respectively; P^{-1} is the inverse of the phenotypic variance-covariance matrix; G is the genotypic variance-covariance matrix.

The resulting index is expressed as:

$$I = b_1X_1 + b_2X_2 + b_3X_3 + b_4X_4$$

Where the b's and the X's are the index weights and the

average phenotypic values of grain yield, grain moisture, root lodging and stalk lodging, respectively.

The phenotypic and genotypic variances and covariances were estimated for each of the cycles considered. The three selection indices were calculated either by using the parameter estimates of the particular cycle of selection or by pooling the parameter estimates of that particular cycle with one or more of the previous cycles. Parameters were estimated by pooling two, three or four consecutive cycles including the cycle under selection.

Pooling of parameter estimates was done with the following formula.

$VC_p = \{\Sigma_{i=1}^{c} VC_i/var(VC_i)\}/\Sigma_{i=1}^{c} (1/var(VC_i)$ (T. B. Bailey, Department of Statistics, Iowa State University, personal communication, 1989).

where VC_p is the pooled variance or covariance; c is the number of cycles combined; VC_i is the variance or covariance component of the i-th cycle; and $var(VC_i)$ is the variance of VC_i.

The variance of the variance or covariance components were estimated using formulae presented by Baker (1986) and Becker (1984).

Selection was practiced in three cycles of the half-sib family selection and in four cycles of the selfed family selection using selection indices obtained with the different

combinations of pooled variances and covariances, for each of the three Smith-Hazel indices. Selection differentials, expressed as a percentage of the selection differentials obtained with single trait selection, were calculated for each selection index in each cycle of selection. Also, predicted genetic gains for each trait and the aggregate genotype were calculated by using the following formulae: $\underline{D} = k\underline{G}\underline{b}/(\underline{b}'\underline{P}\underline{b})^{1/2}$ and $DH = \underline{a}'\underline{D}$ (Lin, 1978) where $\underline{D}$ is a vector of traits genetic gains; k is the standardized selection differential; G and P are the genetic and phenotypic variance-covariance matrices, respectively; $\underline{b}$ is the vector of index weights; DH is the gain in the aggregate genotype; and $\underline{a}$ is a vector of "economic weights".

Results and Discussion

The three Smith-Hazel indices each showed a reduction in the selection differentials for at least one of the traits in all cycles of half-sib family selection, except in cycle 5, when selection was performed with indices estimated from pooled variances and covariances (Table 1). A large reduction in the selection differential was observed for root lodging in cycle 4 for the SHY and in all three cycles of selection for the other selection indices (SHSD and SHE). Similar results

Table 1. Selection differentials, expressed as a percentage of the single-trait selection differentials, for grain yield, grain moisture, root lodging and stalk lodging for three selection indices calculated by pooling information from several cycles of selection. Half-sib family selection

Index	Cycles combined[a]	Cycle of selection[b]	Grain yield	Grain moisture	Root lodging	Stalk lodging
SHY	1	C4	52.9	58.2	-16.7	87.3
	2	C4	36.7	52.4	-37.0	97.6
	3	C4	53.9	54.7	-49.1	91.5
	1	C5	39.9	16.6	49.5	87.6
	2	C5	47.3	27.3	43.6	83.7
	3	C5	39.9	16.5	49.5	87.3
	4	C5	39.9	16.5	49.5	87.3
	1	C6	36.3	74.3	31.0	53.7
	2	C6	-8.4	25.7	60.9	80.5
	3	C6	-9.6	40.8	44.1	86.0
	4	C6	-20.4	34.6	33.5	91.7
SHSD	1	C4	38.8	65.9	-13.7	62.8
	2	C4	36.9	57.6	-36.4	94.3
	3	C4	60.2	77.6	-64.2	63.6
	1	C5	56.0	32.4	41.1	75.4
	2	C5	36.0	41.7	41.7	79.6
	3	C5	38.5	31.7	24.9	89.1
	4	C5	45.1	47.5	27.7	71.9
	1	C6	36.3	74.3	31.0	53.7
	2	C6	1.4	49.2	22.9	88.6
	3	C6	1.4	49.2	22.9	88.6
	4	C6	-9.4	43.0	12.4	94.3
SHE	1	C4	40.0	45.9	-33.2	97.8
	2	C4	36.7	52.4	-37.0	97.6
	3	C4	60.2	52.4	-63.6	89.3

[a]Number of cycles from which pooled variances and covariances were obtained.
[b]Cycle in which selection was practiced.

Table 1. (continued)

Index	Cycles combined[a]	Cycle of selection[b]	Grain yield	Grain moisture	Root lodging	Stalk lodging
SHE	1	C5	89.9	-23.0	25.9	64.5
	2	C5	71.2	9.4	24.0	83.4
	3	C5	70.2	5.8	8.4	87.3
	4	C5	87.2	-18.0	19.0	70.4
	1	C6	-8.4	25.7	60.9	80.5
	2	C6	13.4	35.2	31.4	83.8
	3	C6	3.6	40.8	30.2	86.9
	4	C6	-1.4	38.0	-7.7	96.5
				Average		
SHY	1	C4-C6	43.0	49.7	21.3	76.2
	2	C4-C6	25.2	35.1	22.5	87.3
	3	C4-C6	28.1	37.3	14.8	88.3
	4	C5-C6	9.8	25.6	41.5	89.5
SHSD	1	C4-C6	43.7	57.5	19.5	64.0
	2	C4-C6	24.8	49.5	9.4	87.5
	3	C4-C6	33.4	52.8	-5.5	80.4
	4	C5-C6	17.8	45.2	20.0	83.1
SHE	1	C4-C6	40.5	16.2	17.9	80.9
	2	C4-C6	40.4	32.3	6.1	88.3
	3	C4-C6	44.7	33.0	-8.3	87.8
	4	C5-C6	42.9	10.0	5.6	83.4

were obtained for grain yield in cycle 6 when selection was done using SHY and SHSD. The selection differentials for stalk lodging were improved by pooling in cycle 6 of all three indices. However, the improvement came at the expense of drastically reducing the selection differentials for yield and the other traits, producing uneven responses among the traits

in the index. Generally, any increases in selection differentials obtained by pooling for one trait were offset by decreases in the selection differentials for other traits. An exception was observed in cycle 5, where the SHY index calculated using pooled variances and covariances from two cycles produced increases in the selection differentials for grain yield and grain moisture, while little change was observed in the selection differentials for root lodging and stalk lodging. On the average, none of the indices calculated by pooling variances and covariances from different cycles gave better results, for the simultaneous improvement of the four traits considered, than those observed with the indices calculated using the parameter estimates specific to the cycle in which selection was practiced.

The results for the selfed family recurrent selection program were similar to the results observed for the half-sib family selection program (Table 2). Reduction in the selection differentials when using selection indices calculated by pooling information from different cycles were obtained for some traits and cycles of selection. This was observed for grain yield in cycles 2, 3 and 4 for the three selection indices. This was also observed for grain moisture in all cycles of selection in the SHY index, and in cycles 2, 3 and 5 of the SHSD index. Pooling information from two cycles gave better results for cycle 3 in SHY and SHE than

Table 2. Selection differentials, expressed as a percentage of the single-trait selection differentials, for grain yield, grain moisture, root lodging and stalk lodging for three selection indices calculated by pooling information from several cycles of selection. Selfed family selection

Index	Cycles combined[a]	Cycle of selection[b]	Grain yield	Grain moisture	Root lodging	Stalk lodging
SHY	1	C2	0.2	62.9	75.0	73.8
	2	C2	-43.3	39.0	88.2	81.1
	3	C2	-26.7	29.7	54.8	94.8
	1	C3	69.6	39.8	74.4	45.8
	2	C3	49.9	47.7	72.4	56.4
	3	C3	-10.6	6.4	60.3	97.8
	4	C3	-10.6	6.4	60.3	97.8
	1	C4	10.3	68.9	82.4	79.1
	2	C4	-18.2	43.6	97.4	13.2
	3	C4	-21.6	50.6	94.2	18.6
	4	C4	-24.4	28.6	-9.8	100.0
	1	C5	34.1	50.3	86.1	58.3
	2	C5	51.0	6.4	71.7	60.7
	3	C5	33.3	6.8	93.7	63.2
	4	C5	33.5	7.4	91.9	60.8
SHSD	1	C2	12.5	66.4	72.7	64.1
	2	C2	-25.1	48.3	67.1	89.9
	3	C2	-25.1	48.3	67.1	89.9
	1	C3	69.7	60.9	51.3	22.7
	2	C3	62.1	63.5	37.2	48.7
	3	C3	7.5	6.4	70.5	95.2
	4	C3	9.2	8.3	70.5	94.5
	1	C4	41.0	59.8	45.7	83.2
	2	C4	7.0	65.1	94.7	34.6
	3	C4	7.0	65.1	94.7	34.6
	4	C4	-28.7	39.4	91.8	34.4

[a]Number of cycles from which pooled variances and covariances were obtained.
[b]Cycle in which selection was practiced.

Table 2. (continued)

Index	Cycles combined[a]	Cycle of selection[b]	Grain yield	Grain moisture	Root lodging	Stalk lodging
SHSD	1	C5	26.4	53.8	85.1	64.4
	2	C5	55.4	6.8	55.3	59.6
	3	C5	42.4	7.6	97.0	60.4
	4	C5	33.7	9.2	95.5	62.0
SHE	1	C2	40.3	28.2	61.4	73.5
	2	C2	-13.0	16.6	41.1	95.1
	3	C2	36.1	23.6	56.8	77.2
	1	C3	93.3	-1.9	24.4	41.3
	2	C3	79.7	12.0	42.3	51.5
	3	C3	71.8	17.3	34.6	65.9
	4	C3	80.2	22.9	22.4	58.5
	1	C4	60.2	3.3	38.2	73.6
	2	C4	25.2	27.8	76.0	41.3
	3	C4	25.2	27.8	76.0	41.3
	4	C4	21.3	21.6	72.8	51.1
	1	C5	76.4	-20.6	67.7	59.9
	2	C5	84.6	-5.8	58.8	54.0
	3	C5	77.7	-6.2	84.8	52.7
	4	C5	77.7	-6.2	84.8	52.7
				Average		
SHY	1	C2-C5	28.6	55.5	79.5	64.2
	2	C2-C5	9.8	34.2	82.4	52.8
	3	C2-C5	-6.4	23.4	75.8	68.6
	4	C3-C5	-0.5	14.1	47.5	86.2
SHSD	1	C2-C5	37.4	60.2	63.7	58.6
	2	C2-C5	24.8	45.9	63.6	58.2
	3	C2-C5	8.0	31.8	82.3	70.0
	4	C3-C5	4.7	19.0	85.9	63.6
SHE	1	C2-C5	67.6	2.2	48.0	62.1
	2	C2-C5	44.1	12.6	54.6	60.5
	3	C2-C5	52.7	15.6	63.0	59.3
	4	C3-C5	59.7	12.8	60.0	54.1

using the selection index calculated with the parameter estimates specific to that cycle of selection. On the average, none of the selection indices calculated with pooled data were observed to have selection differentials better than the selection indices calculated with data of the specific cycle of selection.

There was close agreement between predicted genetic gains for half-sib family selection (Table 3) and selection differentials (Table 1) for each of the traits. Generally, as selection differentials increased or decreased with pooling a corresponding increase or decrease was observed for the predicted genetic gains. However, there were some exceptions. The most obvious exception was for grain yield in cycle 6 of the SHY index calculated with pooled data; the predicted genetic gains were in the desired direction but the selection differentials were in the undesired direction. When the predicted genetic gains were averaged over cycles of selection, there was close agreement between selection differentials and predicted genetic gains for individual traits. Selection differentials in the desired direction were usually associated with predicted genetic gains in the desired direction.

Generally, predicted genetic gain in the aggregate genotype for half-sib family selection decreased as the number of cycles included in the parameter estimates increased.

Table 3. Predicted genetic gains for grain yield, grain moisture, root lodging stalk lodging, and aggregate genotype (H) for three selection indices calculated by pooling information from several cycles of selection. Half-sib family selection

Index	Cycles combined[a]	Cycle of selection[b]	Grain yield	Grain moisture	Lodging Root	Lodging Stalk	H
SHY	1	C4	0.74	-0.92	-0.15	-7.49	3.41
	2	C4	0.74	-0.87	0.69	-6.89	2.71
	3	C4	1.25	-0.90	1.22	-1.56	1.91
	1	C5	0.56	0.12	-1.17	-1.35	3.23
	2	C5	0.63	-0.23	-0.89	-1.51	3.30
	3	C5	0.45	-0.17	-0.57	-1.62	2.96
	4	C5	0.47	-0.12	-0.58	-1.33	2.84
	1	C6	1.21	-0.87	-2.35	-6.46	3.38
	2	C6	0.79	-0.15	-1.08	-1.35	3.32
	3	C6	0.75	-0.38	-0.88	-1.54	3.38
	4	C6	0.48	-0.34	-0.53	-1.66	3.03
SHSD	1	C4	0.80	-0.97	0.12	-7.78	2.35
	2	C4	0.66	-0.99	0.71	-6.49	1.83
	3	C4	0.98	-1.13	1.04	-1.09	1.20
	1	C5	1.24	-0.24	-0.59	-0.97	1.27
	2	C5	0.75	-0.58	-0.39	-1.24	1.57
	3	C5	0.39	-0.62	-0.10	-1.33	1.37
	4	C5	0.57	-0.70	0.02	-0.88	1.19
	1	C6	1.33	-0.94	-1.67	-6.45	2.20
	2	C6	1.61	-0.53	-0.44	-0.93	1.56
	3	C6	1.06	-0.68	-0.35	-1.27	1.71
	4	C6	0.71	-0.71	-0.01	-1.37	1.51
SHE	1	C4	0.90	-0.65	0.22	-8.82	10.15
	2	C4	1.10	-0.60	0.87	-7.36	8.19
	3	C4	1.89	-0.50	1.55	-1.89	2.74

[a]Number of cycles from which pooled variances and covariances were obtained.
[b]Cycle in which selection was practiced.

Table 3. (continued)

Index	Cycles combined[a]	Cycle of selection[b]	Grain yield	Grain moisture	Lodging Root	Lodging Stalk	H
SHE	1	C5	3.84	0.61	-0.34	-0.92	4.49
	2	C5	1.76	0.08	-0.42	-1.50	3.60
	3	C5	1.50	0.11	-0.06	-1.65	3.10
	4	C5	1.75	0.13	0.05	-1.30	2.87
	1	C6	0.20	-0.44	-3.43	-8.26	12.33
	2	C6	3.41	0.19	-0.27	-0.99	4.47
	3	C6	1.98	-0.08	-0.35	-1.51	3.92
	4	C6	1.74	-0.06	0.07	-1.67	3.39
					AVERAGE		
SHY	1	C4-C6	0.84	-0.56	-1.22	-5.10	3.34
	2	C4-C6	0.72	-0.42	-0.43	-3.25	3.11
	3	C4-C6	0.82	-0.48	-0.08	-1.57	2.75
	4	C5-C6	0.48	-0.23	-0.56	-1.50	2.94
SHSD	1	C4-C6	1.12	-0.72	-0.71	-5.07	1.94
	2	C4-C6	1.01	-0.70	-0.04	-2.89	1.65
	3	C4-C6	0.81	-0.81	0.20	-1.23	1.43
	4	C5-C6	0.64	-0.70	0.01	-1.12	1.35
SHE	1	C4-C6	1.65	-0.16	-1.18	-6.00	8.99
	2	C4-C6	2.09	-0.11	0.06	-3.28	5.42
	3	C4-C6	1.79	-0.16	0.38	-1.68	3.25
	4	C5-C6	1.74	0.04	0.06	-1.48	3.13

There were only two exceptions to this pattern. In cycle 5, the SHY and SHSD indices calculated using data combined from two cycles had higher predicted gains for the aggregate genotype when compared with the same indices calculated with the parameter estimates from the specific cycle of selection. Averaged over cycles, there was a decrease in the predicted

genetic gains for the aggregate genotype as the number of cycles included in the parameter estimates increased.

The results from selfed family selection also showed close agreement between selection differentials (Table 2) and predicted genetic gains (Table 4) for individual traits. Increases or decreases in the selection differentials were associated with corresponding increases or decreases in the predicted genetic gains. Exceptions to this pattern were observed for cycle 4 of the SHY index when data from four cycles were pooled. In this case, a selection differential in the undesired direction was obtained for root lodging but the predicted genetic gain was in the desired direction. The same result was observed for grain yield in cycle 2 of the SHE index. Averaged over cycles, there was good agreement between selection differentials and predicted genetic gains for individuals traits.

For the predicted gain in the aggregate genotype, an increase was observed for the SHY and SHSD as the number of cycles combined increased, except for cycle 5 in the SHSD index for which a decrease was observed. Predicted genetic gains in aggregate genotype for the SHE index decreased for cycles 2, 4, and 5 as the number of cycles included in the parameter estimates increased, but an increase was observed for cycle 3. Averaged over cycles, and increase in predicted genetic gains was observed for the SHY and SHSD indices as the

Table 4. Predicted genetic gains for grain yield, grain moisture, root lodging stalk lodging, and aggregate genotype (H) for three selection indices calculated by pooling information from several cycles of selection. Selfed family selection

Index	Cycles combined[a]	Cycle of selection[b]	Grain yield	Grain moisture	Lodging Root	Lodging Stalk	H
SHY	1	C2	-1.39	-0.97	-3.37	-5.84	2.60
	2	C2	-1.77	-0.67	-4.38	-1.19	3.73
	3	C2	-1.14	-0.98	-4.70	-0.86	3.48
	1	C3	1.87	-0.47	-0.71	-1.32	2.77
	2	C3	0.19	-0.76	-0.98	-2.80	2.78
	3	C3	-1.58	-0.32	-3.31	-0.82	5.87
	4	C3	-1.00	-0.58	-2.42	-1.12	5.46
	1	C4	-0.26	-0.93	-2.30	-5.22	3.40
	2	C4	0.68	-0.76	-0.75	-3.34	3.00
	3	C4	-0.21	-0.86	-1.00	-3.95	2.93
	4	C4	-2.51	-0.22	-4.42	-0.27	6.06
	1	C5	3.18	-0.78	-3.93	-5.09	3.08
	2	C5	1.11	-0.80	-3.84	-4.62	2.87
	3	C5	1.29	-0.90	-1.08	-4.06	3.34
	4	C5	0.43	-0.96	-1.30	-4.64	3.26
SHSD	1	C2	-1.17	-1.22	-3.10	-5.02	1.59
	2	C2	-1.03	-1.13	-4.24	-0.93	1.95
	3	C2	0.66	-1.52	-3.90	-0.58	1.88
	1	C3	2.97	-1.10	-0.51	0.50	1.15
	2	C3	1.23	-1.19	-0.78	-1.28	1.27
	3	C3	-0.26	-0.80	-2.13	-1.15	2.17
	4	C3	0.63	-1.11	-1.94	-0.95	2.11
	1	C4	0.68	-0.96	-1.97	-4.70	1.51
	2	C4	1.52	-0.98	-0.61	-2.50	1.36
	3	C4	0.67	-1.08	-0.84	-3.06	1.41
	4	C4	-0.54	-0.78	-1.65	-1.43	2.10

[a]Number of cycles from which pooled variances and covariances were obtained.
[b]Cycle in which selection was practiced.

Table 4. (continued)

Index	Cycles combined[a]	Cycle of selection[b]	Grain yield	Grain moisture	Lodging Root	Lodging Stalk	H
SHSD	1	C5	2.35	-0.91	-3.77	-5.39	2.09
	2	C5	0.93	-0.88	-3.35	-5.10	1.86
	3	C5	1.50	-1.03	-0.94	-3.96	1.74
	4	C5	0.81	-1.10	-1.14	-4.28	1.76
SHE	1	C2	1.32	0.04	-2.58	-6.28	10.14
	2	C2	5.11	-0.27	-2.66	-0.09	8.13
	3	C2	6.22	-0.69	-1.83	-0.10	8.84
	1	C3	4.13	0.04	-0.33	-1.13	5.55
	2	C3	3.88	0.21	-0.45	-2.36	6.48
	3	C3	5.54	-0.34	-0.77	-0.07	6.73
	4	C3	6.43	-0.61	-0.54	0.01	7.57
	1	C4	2.02	-0.07	-1.85	-5.34	9.28
	2	C4	3.26	0.11	-0.46	-3.29	6.91
	3	C4	3.05	0.13	-0.56	-3.73	7.21
	4	C4	5.06	-0.13	-0.84	-0.06	6.08
	1	C5	5.88	0.07	-2.73	-6.30	14.84
	2	C5	3.33	0.08	-2.82	-5.78	11.84
	3	C5	3.96	0.15	-0.56	-5.06	9.44
	4	C5	3.78	0.17	-0.65	-5.26	9.52
				AVERAGE			
SHY	1	C2-C5	0.85	-0.79	-2.58	-4.37	2.96
	2	C2-C5	0.05	-0.75	-2.49	-2.99	3.10
	3	C2-C5	-0.41	-0.76	-2.52	-2.42	3.90
	4	C3-C5	-1.03	-0.59	-2.71	-2.01	4.93
SHSD	1	C2-C5	1.21	-1.05	-2.34	-3.65	1.58
	2	C2-C5	0.66	-1.04	-2.24	-2.45	1.61
	3	C2-C5	0.64	-1.11	-1.95	-2.19	1.80
	4	C3-C5	0.30	-1.00	-1.57	-2.22	1.99
SHE	1	C2-C5	3.34	0.02	-1.87	-4.76	9.95
	2	C2-C5	3.90	0.03	-1.60	-2.88	8.34
	3	C2-C5	4.69	-0.19	-0.93	-2.24	8.06
	4	C3-C5	5.09	-0.19	-0.68	-1.77	7.72

number of cycles included in the parameter estimates increased. These increases were more pronounced for the SHY than for the SHSD. In the SHE index, decreases in the predicted gain in the aggregate genotype were observed as the number of cycles combined increased.

One of the objectives of a recurrent selection program could be the simultaneous improvement of all the traits included in the selection index with equal importance being assigned to each trait. In this case, the best results expected would be when all traits have the same percentage improvement with respect to the maximum attainable when using single-trait selection. When four non-correlated traits are being selected, the expected progress for each trait (based on the results presented by Hazel and Lush in 1942) would be 50% of the expected progress for single-trait selection. In this study, the selection differentials of the traits tended to deviate from the optimum value of 50%, with the deviation being greater when the indices were calculated using pooled information than when using information of the specific cycle of selection.

From the results obtained in this study, neither selection differentials nor predicted genetic gains for the individual traits were observed to be better using selection indices calculated with pooled parameter estimates, when compared with the index calculated using parameter estimates

from the specific cycle in which selection was practiced.

For the predicted gain in aggregate genotype, some contradictory responses were obtained. In some cases, there was an increase in gains when the number of cycles combined increased and in other cases a decrease was observed. One problem in interpreting these results is that the aggregate genotype depends on the economic values used to estimate the selection index. The economic values of the SHY and SHSD depend on the parameter estimates (heritabilities and phenotypic standard deviations) used to calculate them. Because the parameter estimates changed as the number of cycles used for pooling variances and covariances changed, the predicted gains in the aggregate genotype were also expected to change. The SHE is more appropriate for comparing differences in predicted gains in the aggregate genotype because the economic values are the same and the differences observed will be due only to changes in parameter estimates rather than changes in the definition of the aggregate genotype. Predicted genetic gains in the aggregate genotype for the SHE increased as the number of cycles included in the parameter estimates increased for only one cycle of selfed family selection. For all the other cycles of both selection methods the predicted genetic gains decreased as the number of cycles included in the parameter estimates increased.

In general, the Smith-Hazel selection indices calculated

by pooling parameter estimates were neither better for improving the four traits simultaneously nor for improving the aggregate genotype than the selection indices calculated without pooling parameter estimates. Milla and Lamkey (1989) found that when compared to other indices, the Smith-Hazel index is not appropriate for simultaneously improving all four traits. This result is not entirely due to possible errors in parameter estimates, but could be due to the fact that the Smith-Hazel index maximizes the gain in the aggregate genotype without necessarily producing simultaneous improvement in each trait included in the index.

The failure of the selection indices calculated using pooled parameter estimates could be due to either one of two causes. The genetic parameters could have changed due to gene frequency changes resulting from selection introducing biases in the pooled parameter estimates. Or, as Manning (1956) argued, the use of data from the particular cycle of selection may be more effective than using pooled information because the weighting of several traits in an index is a function of the exact environmental conditions in which the crop was grown. In either case, the best approach would be to have parameter estimates as close as possible to the true parameters. One way to achieve this is by increasing the number of genotypes evaluated in each cycle of selection. This approach not only will help in obtaining better parameter

estimates but will also increase the selection intensity without decreasing the number of genotypes selected for recombination. Kauffman and Dudley (1979) and also Miles et al. (1981) found that variance and covariance estimates obtained from the evaluation of 200 half-sib families were sufficiently accurate to be useful in index development and prediction of gain. Baker (1986), based on a review of several studies, found that estimates must be based on a minimum sample of 30 to 40 genotypes. Usually, in recurrent selection programs more than 100 families are evaluated, which could be an indication that fairly good parameter estimates are being obtained, provided that appropriate experimental techniques are being used for those evaluations.

From the results of this study, it can be concluded that the estimated Smith-Hazel selection indices based on pooled variances and covariances from different cycles of selection are not better, and may even be inferior to those calculated using parameter estimates from the specific cycle where selection is being practiced. These results were found for the simultaneous improvement of grain yield, grain moisture, root lodging, and stalk lodging, and for the improvement of the aggregate genotype in corn.

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GENERAL SUMMARY

To improve a population, several traits must be considered at the same time. Populations that perform well for some traits but are undesirable for others will not be used directly or for the extraction of improved genotypes. Selection indices have been proposed as a suitable procedure for multiple-trait selection. The objectives of this study are: 1) to compare the effectiveness of different selection index methods on the simultaneous improvement of grain yield, grain moisture, root lodging and stalk lodging in corn; and 2) to evaluate the effect of pooling phenotypic and genotypic variances and covariances over several cycles of selection on the estimation of a selection index for improving grain yield, grain moisture, root lodging and stalk lodging in corn.

Variations in the phenotypic and genotypic correlations across cycles were observed. These changes in the structure of the correlations affected the performance of the different selection indices included in this study. The selection indices less affected by these changes were the BSD, EWF and RSI resulting in a more even improvement for the four traits considered. They gave the highest number of cycles in which the selection differentials were significant in the favorable direction for all traits. These results suggest that the BSD, EWF and RSI could be used for the simultaneous improvement of

grain yield, grain moisture, root lodging and stalk lodging in corn.

For the Smith-Hazel selection indices developed by using pooled genotypic and phenotypic variances and covariances over several cycles of selection, it was observed that, on the average, none of the selection indices calculated with pooled data gave better selection differentials than the selection index calculated using data of the specific cycle of selection. Predicted genetic gains for the individual traits considered were, on the average, in good agreement with the results obtained for the selection differentials.

If the selection objective is to improve the aggregate genotype, the Smith-Hazel index should be used provided that good parameter estimates and economic values are available. But, if the simultaneous improvement of all four traits is desired, either BSD, EWF or RSI should be preferred over any of the other indices evaluated in this study.

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